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Advancing research on alien species and biological invasions

Pathologists and entomologists must join forces against forest pest and pathogen invasions

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Abstract

The world's forests have never been more threatened by invasions of exotic pests and pathogens, whose causes and impacts are reinforced by global change. However, forest entomologists and pathologists have, for too long, worked independently, used different concepts and proposed specific management methods without recognising parallels and synergies between their respective fields. Instead, we advocate increased collaboration between these two scientific communities to improve the long-term health of forests.

Our arguments are that the pathways of entry of exotic pests and pathogens are often the same and that insects and fungi often coexist in the same affected trees. Innovative methods for preventing invasions, early detection and identification of non-native species, modelling of their impact and spread and prevention of damage by increasing the resistance of ecosystems can be shared for the management of both pests and diseases.

We, therefore, make recommendations to foster this convergence, proposing in particular the development of interdisciplinary research programmes, the development of generic tools or methods for pest and pathogen management and capacity building for the education and training of students, managers, decision-makers and citizens concerned with forest health.

Keywords

Capacity building, detection, disease, exotic, fungi, forest health, identification, insects, interdisciplinarity, management

The United Nations General Assembly declared the year 2020 as the International Year of Plant Health (IYPH). We take this unique opportunity to affirm that the phytosanitary protection of forests, which is essential for the maintenance of their functions (e.g. climate regulation, wood production, biodiversity reservoir) and, ultimately, for human well-being, requires the joint effort of entomologists and pathologists to prevent or manage severe pest and pathogen problems. In a year characterised by a global threat to human health from the COVID 19 coronavirus pandemic, attention to plant health could be considered derisory. We believe, however, that plants face similar threats and that trees and forests, in particular, play an essential role in providing humans with important services that fit within the concept of "One health" (Xie et al. 2017), because humans will suffer if trees disappear from the landscape.

Throughout the article, we will use as a definition of "pests" insect herbivores that inflict damage to trees and as "pathogens" microorganisms that cause disease to trees, including fungi, oomycetes, bacteria, viruses and nematodes.

Forests under biotic threat

Due to global change, the world's forests are exposed to unprecedented threats from biotic hazards (Simler-Williamson et al. 2019). The increase in volume and acceleration of global trade and travel has boosted the risk of invasion by non-native species into forests (Roy et al. 2014). On all continents, the number of non-native forest insects (Hurley et al. 2016; Brockerhoff and Liebhold 2017) and pathogens (Santini et al.

2013; Ghelardini et al. 2017) that have become established outside their natural range has increased dramatically and this trend shows no signs of levelling off (Seebens et al. 2017). Currently, the greatest damage in forests is often caused by these invasive alien species, including insect pests, such as the Eurasian woodwasp and its associated decay fungus (Hurley et al. 2007), the emerald ash borer (Poland et al. 2006), the polyphagous shot hole borer and its associated fungal pathogens (Paap et al. 2018), the Asian longhorn beetle (Haack et al. 2010) and pathogens, such as the causal agents of sudden oak death (Davidson et al. 2003), ash dieback (Gross et al. 2014), rapid ohia decline (Barnes et al. 2018), Dutch elm disease or the pine wilt disease (Soliman et al. 2012), the latter two being vectored by insects.

Many aspects of climate change promote the emergence of native forest pests and pathogens, foster epidemics and trigger outbreaks in a number of ways. Warmer temperatures may favour winter survival and accelerate the rate of development of many fungi and insects (Robinet and Roques 2010; Santini and Ghelardini 2015; Pureswaran et al. 2018; Jactel et al. 2019; Lehmann et al. 2020). A higher number of generations per year, or increased reproduction rates in univoltine species, results in accelerated population growth. Increase in winter temperatures releases constraints on year-to-year survival of some insect and pathogen species (Marçais et al. 1996; Aguayo et al. 2014), leading to range expansions towards higher elevation and latitudes in the northern hemisphere (Bergot et al. 2004; Battisti et al. 2005; Lehmann et al. 2020). In addition to the warming trend, increasing numbers of extreme events are occurring (IPCC 2012), which also contribute to these epidemics. More frequent or severe droughts lead to water stress on trees (Greenwood et al. 2017), making them more susceptible to opportunistic insect pests and pathogens (Desprez-Loustau et al. 2006; Jactel et al. 2012). Intense windstorms (Gardiner et al. 2013) provide sudden substantial increases in breeding substrates for bark beetles and substrates for fungal infection, which can build up large populations and eventually kill many standing trees (Seidl et al. 2017). Large and severe fires associated with warm and dry conditions, more frequent in a warming climate, may also favour insect outbreaks (Halofsky et al. 2020) and, conversely, trees killed by pests and pathogens may fuel forest fires (Jenkins et al. 2008). Climate change can affect upper trophic levels in different ways, leading to idiosyncratic responses. Parasitoids, for example, may respond positively to temperature increases (Péré et al. 2013), which may explain the decrease in damage observed in some key pest species (Lehmann et al. 2020). Furthermore, climate change, not only provides improved opportunities for many native species, but also invasive alien species from warmer regions (Walther et al. 2009).

Both alien and emerging native forest pests and pathogens have had and will continue to have profound impacts on forest vitality and the economy (Aukema et al. 2011; Ramsfield et al. 2016; Stenlid and Oliva 2016). Yet, the need for forest ecosystems to meet the increasing global demand for biosourced materials and products, to preserve biodiversity (Myers et al. 2000), to contribute to climate change mitigation (Griscom et al. 2017) and the provision of other forest ecosystem services has never been greater. This increasing demand can itself be a factor contributing to new disease

risks, for example, with the development of extensive plantations of exotic trees, where introduced tree species are exposed to resident pests and pathogens to which they have not evolved resistance (Wingfield et al. 2008; Burgess and Wingfield 2015). Moreover, intensification of forestry practices is often associated with reduced stand heterogeneity, especially reduced tree species and genetic diversity (with clonal forestry at the extreme), which may strongly increase pest and pathogen risk (Desprez-Loustau et al. 2016; Persoons et al. 2017; Jactel et al. 2017).

There is clearly an urgent need to develop a common framework to understand insect and pathogen invasions and to develop methods for forest protection that are effective against both tree pests and pathogens. However, forest entomologists and forest pathologists have traditionally followed different conceptual and methodological approaches to understand the epidemiology of pests and pathogens (Wingfield et al. 2017) and they have developed different management approaches for their subjects of study (Raffa et al. 2020). Consequently, the number of scientific papers simultaneously addressing insect pests and fungal pathogens is low. This can be illustrated using the published content from two major journals taken as examples and which specialise separately in pathology and entomology, respectively: Forest Pathology (previously European Journal of Forest Pathology) and Agricultural and Forest Entomology. An average of 11% of papers from the last thirteen years of Forest Pathology mentioned insects in their title, key words or abstract (Fig. 1A) and 10% of papers, published since the first issue of Agricultural and Forest Entomology, mentioned pathogens (Fig. 1B). In both journals, the number of papers has increased with time while the proportion of papers intersecting the disciplines of pathology and entomology remains low and stable.

Data were obtained from a keyword search of the Web of Science database on 8 March 2020, using the following searches "[(((forest pathology) or (European journal of forest pathology)) AND TOPIC: ((insect* or pest or herbivor* or beetle or scolyt* or moth))] and [(agricultural and forest entomology) AND TOPIC: (forest or tree or oak or pine or birch or spruce or fir or beech or maple) AND TOPIC: (fung* or (fungal pathogen*) or (fungal disease) or phytophthora)]".

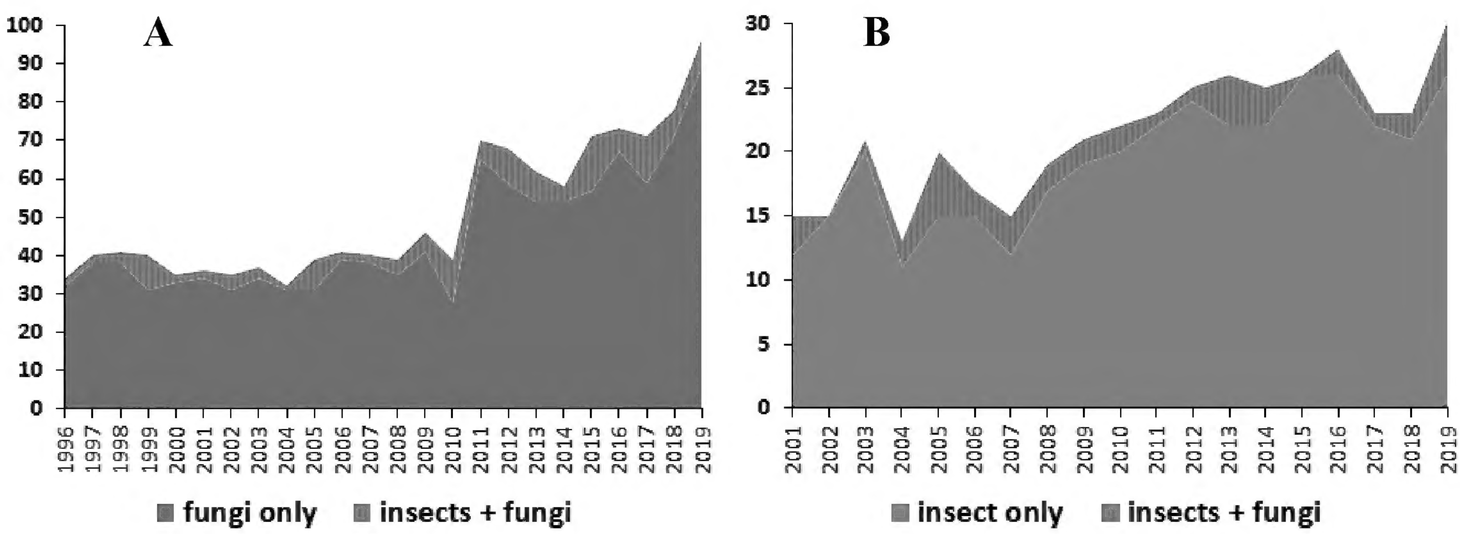

Figure 1. Temporal trend of the number **A** of articles dealing only with forest fungi or with both forest fungi and insects in the (*European Journal of*) *Forest Pathology* (1996–2019) and **B** of articles dealing only with forest insects or with both forest fungi and insects in the journal *Agricultural and Forest Entomology* (2001–2019).

Hereafter, we explain how the conservation of forest health would greatly benefit from more effective cooperation between forest pathologists and forest entomologists and suggest ways to achieve this outcome.

Preparedness and border surveillance

An essential step in the prevention and control of forest pest and pathogen problems is their recognition as potentially damaging agents and preventing their arrival. Ideally, insects and microbes that have the potential to become pests and pathogens should be identified and the damage they cause characterised, before they are introduced to new areas, because this would provide time to develop and implement measures for detection and management. As invasive organisms are frequently associated with plant trade, a commodity risk assessment may be useful and it was recently adopted as a strategic approach by the European Union, with pathologists and entomologists in the same working group (EFSA 2019). Sentinel plantings in exporting countries provide excellent resources for early identification of plant pests and pathogens at high risk of causing damage should they become introduced. Consisting of woody species that are native to importing countries, sentinel plantings can serve to identify the pests and pathogens of highest potential to impact trees in the importing country (Eschen et al. 2019). Studies of tree health in these facilities also represent an ideal opportunity for collaboration between entomologists and pathologists.

Improved knowledge of the pathways of movement and entry of alien organisms is a key step towards improved strategies for preventing arrival of these organisms through quarantine measures. Recent studies have shown that many pathways by which alien forest pests and pathogens move worldwide are shared amongst these organisms, being mainly associated with trade in live trees or germplasm and transport of wood packing material (Liebhold et al. 2012; Ghelardini et al. 2017; Meurisse et al. 2019). Identification of these pathways is crucial for the adoption of measures, such as phytosanitary treatments, to prevent introductions (Allen et al. 2017). Research identifying the wood packaging and live plant invasion pathways has led to global implementation of phytosanitary standards such as ISPM 14 (International Standards For Phytosanitary Measures No. 14, 2019) "The use of integrated measures in a systems approach for pest risk management" and ISPM 15 (2019) "Regulation of wood packaging material in international trade" resulting in tangible decreases in risks of new invasions (Kenny 2002; Leung et al. 2014). However, further work is needed to identify emerging pathways common to pests and pathogens, as well as strategies for mitigating the impacts of these pathways.

New technologies for alien forest pests and pathogens detection and identification

Detection of pests and pathogens at ports of entry is complicated by the volumes of material that are imported and generally a lack of capacity of quarantine officers. Many

emerging technologies could substantially improve this situation (Luchi et al. 2020). For example, many forest insects and pathogenic fungi emit volatile organic compounds sufficiently characteristic to indicate their presence (Nixon et al. 2018). Detection devices for such volatile compounds could be developed (e.g. e-nose), installed in containers at their point of departure and automatically checked at their point of arrival, to help with the screening of large volumes of commodities (Poland and Rassati 2019).

Most alien insect pests and pathogens that cause damage in invaded areas were not known as causes of damage, or even described, in their area of origin (Roques et al. 2015; Burgess and Wingfield 2015). Moreover, many insects and fungi can hardly be identified at species level on the basis of morphology alone, making it difficult to distinguish a potential introduced organism from a closely-related native species, as exemplified by *Hymenoscyphus fraxineus*, the causal agent of ash dieback (Gross et al. 2014) or the brown spruce longhorn beetle (*Tetropium fuscum*) which was not recognised as an exotic in Canada, because of morphological similarity to the native *Tetropium cinnamopterum* (Ramsfield 2016). It is, therefore, essential to develop molecular tools that will allow detection and identification of potentially invasive alien species to be able to set up measures to eradicate them at an early stage (McTaggart et al. 2016). Historically, molecular methods of identification have been more developed for fungal pathogens because it is especially difficult to recognise species, based on morphological features of the fungal spores (Taylor et al. 2000; Pashley et al 2012; Steenkamp et al. 2018). However, the same difficulties apply to the recognition of insect immature forms such as larvae. Cooperation between forest entomologists, pathologists and molecular biologists would accelerate the development of pipelines for the rapid identification of these unknown organisms (Feau et al. 2011; Malacrinò et al. 2017). In addition, emerging molecular methods, based on metabarcoding, may allow the characterisation of entire communities, which offers great prospects for surveillance of both pests and pathogens, based on environmental samples (e.g. eDNA; Aguayo et al. 2018; Piper 2019).

Another approach that should be shared by plant pathologists and entomologists is risk modelling. Quantitative pest and pathogen risk assessment is recommended, because it allows various risk reduction options to be tested in order to enable decision support schemes (EFSA PLH Panel 2018) while quantifying uncertainty levels. This approach follows the same steps as those of the invasion process (i.e. arrival, establishment, spread and impact) and, therefore, makes it possible to prioritise the areas or products to be monitored as a matter of priority, which ultimately optimises early detection (Robinet et al. 2012; Douma et al. 2015; Gottwald et al. 2019). Clearly, forest pathologists and entomologists can work together using such a methodology for forecasting and their cooperation will help to take into account multiple hazards to strengthen the conclusions of these quantitative risk analyses.

Post-border surveillance

Despite efforts to prevent potentially damaging species from arriving, many such organisms will evade detection and potentially establish alien populations. Early de-

tection of nascent populations is critical to the success of attempts to eradicate such populations and integrated surveillance programmes therefore play a key role in national biosecurity programmes (Coulston et al. 2008; Pluess et al. 2012; Liebhold et al. 2016). Surveillance for arrivals of alien forest pests and pathogens should focus in high-risk areas, such as urban and peri-urban forests close to industrial and commercial areas and near ports and airports (Branco et al. 2019). Characterisation of geographical variation in invasion risk and optimal allocation of surveillance resources across that variation is critical to the success of surveillance programmes (Epanchin-Niell 2017).

The isolation and identification of pheromones and other semiochemicals has played a key role in providing trapping technologies used in insect surveillance programmes (Poland and Rassati 2019). Combining multiple lures, targeting various pest species in a single trap, holds great potential in the development of integrated pest surveillance programmes (Brockerhoff et al. 2013). Spore-trapping, stream baiting and other technologies also hold potential for integration of tree pathogen detection in national biosecurity programmes (Sutton et al. 2009; Botella et al. 2019). Increasingly, citizen science projects have become important for detection and surveillance in many countries. Importantly, the efficacy of these projects, as well as the confirmation of records received, requires expert backing from the disciplines of both entomology and plant pathology. This is particularly true in the case of web applications that require the public to report any form of damage observed in trees, as, for example, in the Silvalert (www.silvalert.net) and Treealert (https://treealert.forestresearch.gov.uk) projects. Strong communication and data sharing within and between countries is essential to prepare for emerging threats to forests. The European Union EUROPHYT platform is a leading example of such best practice for official notifications and rapid alerts, as are the databases provided by CABI and EPPO.

Interactions between organisms on host trees

For many pathogens, transmission and/or introduction into the host by an insect vector is essential for infection and spread (Wingfield et al. 2016; Santini and Battisti 2019). Insect vectoring is the main if not sole way of dissemination of many important vascular pathogens, such as *Xylella fastidiosa*, the cause of Bacterial Leaf Scorch, vectored by leafhoppers and froghoppers (Landa et al. 2020), *Ophiostoma novo-ulmi*, the agent of Dutch Elm Disease, vectored by elm bark beetles (McLeod et al. 2005) and the pine wilt nematode, *Bursaphelenchus xylophilus*, vectored by *Monochamus* longhorn beetles (Sousa et al. 2001). In the case of bacteria, insects may serve as alternative primary hosts (Nadarasah and Stavrinides 2011).

It is increasingly acknowledged that insects and microbes interact in and on their host trees. Insect infestation can predispose trees to attack by fungal pathogens, increasing damage caused by the pathogens and enabling weaker pathogens to attack hosts (Xi et al. 2018). Some forest insects are known to carry various species of fungi that they use as symbionts for larval development (Ramsfield 2016), "cultivate" and use for food in the galleries they form in the tree (e.g. ambrosia beetles) or to overcome

the induced defences of colonised trees (e.g. bark beetles) (Six and Wingfield 2011). In some cases, fungal associates of beetles are tree pathogens (Hulcr et al. 2011), which can explain the high rate of tree mortality recently caused by the massive attacks of the polyphagous shot hole borer (Paap et al. 2018). Diseases associated with ambrosia and bark beetles and their symbiotic fungi are amongst the most important emerging problems affecting tree health in the last century (Ploetz et al. 2013, Fig. 2).

In contrast with their mutualistic relationships, insects may be natural enemies of pathogenic fungi, with some species being putative obligate mycophages (Dillen et al. 2017). Additionally, fungal tree infection by biotrophic pathogens and endophytes can reduce insect performance on challenged trees (Fernandez-Conradi et al. 2018). Fungi may have direct toxic effects on insects, being entomopathogens (Dowd 2000) or indirect tree-mediated effects through reduced nutritional quality or induction of systemic defences against herbivores. It is known that plants use cost-effective inducible defences to protect against insects and pathogens, whilst the latter have developed mechanisms to overcome and/or manipulate those defences to their benefit. Both insects and fungi can trigger host plant defence responses through the biochemical pathways of jasmonic acid (JA), salicylic acid (SA) and ethylene (ET). Many examples exist where JA and SA can interact antagonistically (Thaler et al. 2012) and recent insights suggest they could also interact synergistically (Liu et al. 2016). During multi-attack events, the activation of defences towards one attacker can increase or reduce susceptibility to the other (Vos et al. 2013; Castagneyrol et al. 2018). Although our knowledge regarding plant defences in crop systems has improved in recent years, the study of defence mechanisms against both insects and pathogens in forest trees is only beginning to emerge.

Symbiosis between trees and mycorrhizae can modify tree physiology and tree-insect interactions (Koricheva et al. 2009), with effects depending on the feeding guild

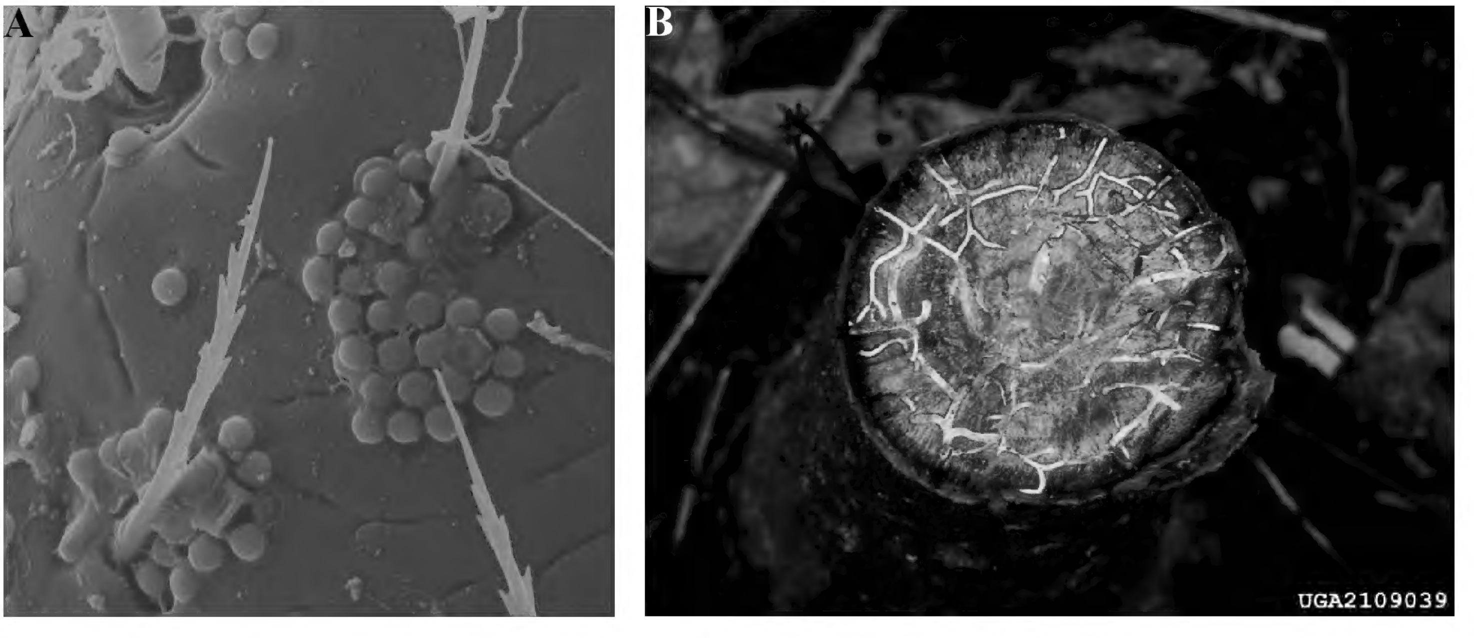

Figure 2. Examples of interactions between forest insects and fungi **A** detail of the abdomen of the ambrosia beetle *Xyleborinus saxesenii* (Ratzeburg, 1837) from below with fungal spores (Courtesy of Peter Biedermann, University of Freiburg, Germany) **B** mycelium filling the galleries of the ambrosia beetle *Xyleborus glabratus* (Eichhoff, 1877) (Courtesy of James Johnson, Georgia Forestry Commission, Bugwood.org).

of the insect and the type of mycorrhizae. Likewise, interactions between mycorrhizae and plant pathogens should not be overlooked, as rhizosphere fungi have the potential to exclude, outcompete or enhance the defence system of plants to more effectively respond to invading pathogens (Selosse 2014). However, it remains largely unknown how the complex interactions between the tree and its microbiome, which forms the holobiont, affect tree susceptibility to pests and pathogens (Vivas et al. 2015; Mishra et al. 2020). This necessitates a more holistic approach to understanding of biotic interactions involving insects, fungi, oomycetes, viruses and bacteria at both the individual tree and forest levels and their consequences for forest health (Naidoo et al. 2019).

Control measures of forest pests and pathogens

Once they have attacked a tree, both insects and pathogens are often difficult to locate for treatment. Most species are inconspicuous, living under the bark or within tissues, such as bark beetles and leaf miners or vascular fungi and root pathogens. External feeders (e.g. defoliators) or diseases (e.g. leaf rusts) are located in the crowns of trees that are tens of metres above the ground. This makes it difficult and often ineffective to apply insecticides and fungicides. Indeed, pesticides are typically not effective at controlling forest insect and disease outbreaks at a regional scale (Liebhold 2012). The negative effects of pesticides on human health and the environment and the risk of pests and pathogens developing resistance to them, are receiving more attention. This has led to their rejection by the public and bans on their use in forests by the authorities, as has occurred with neonicotinoids in Europe (Jactel et al. 2019). There is consequently a common need for alternative control methods against tree pests and pathogens.

Preventative control measures should be favoured and previous studies have shown that adapting forest management to reduce stand susceptibility is the most promising approach. For example, selecting tree species suitable for future pedoclimatic conditions, as well as initial fertilisation and regular thinning, are methods that can increase the vigour of individual trees and could improve their resistance to secondary insects and pathogens (Jactel et al. 2009). Increasing tree species diversity improves forest resistance (i.e. associational resistance) by various bottom-up and top-down mechanisms such as reducing the likelihood of propagules reaching host trees and promoting the control of pests and pathogens by their natural enemies (Jactel et al. 2017; Grosdidier et al. 2020). However, the direction and magnitude of the effect of host species diversity on disease incidence (the so-called "dilution effect" when negative) remains controversial and contrasting evidence exists (Liu et al. 2020). An improved understanding of the effect of biodiversity on forest vulnerability to damaging biotic agents and joint research between entomologists and pathologists are required to identify the silvicultural and land use management practices that could effectively reduce the impact of multiple damaging agents.

Where alien pests and pathogens become established and multiply too rapidly in an area to be eradicated, then the priority shifts to preventing or slowing their further

spread. Common features have been identified that influence the invasibility (resistance to invasion) of forest landscapes by non-native insects and pathogens. In particular, there is mounting evidence that a homogeneous forest landscape with a high proportion of the main host species, in the form of large monocultures or large connected patches, would favour the rapid spread of forest pests and pathogens (Condeso and Meentemeyer 2007; Morin et al. 2009; Rigot et al. 2014; Haas et al. 2016; Hudgins et al. 2017; Prospero and Cleary 2017). To further develop and challenge our understanding of these effects and better predict areas at higher risk of contagion, it is important to develop spread models that address both insects and pathogens and to test the simulations in realistic forest landscapes (Robinet et al. 2019; Barron et al. 2020). Although the processes of natural dispersal of organisms differ between insects and fungi, mainly active dispersal by flight for the former and passive dispersal via wind, rain or vectors for the latter, human-assisted dispersal and the barriers to dispersal are similar for both. These are mainly landscape composition (proportion of host and non-host habitats) and fragmentation over short distances and population density and trade networks for human-assisted spread over long distances (Hudgins et al. 2017). As is true for surveillance and early detection, generic modelling frameworks could be developed for both insect pests and pathogens in order to better understand the potential spread of biological invasions, optimise monitoring systems and manage the landscape to reduce their spread rates and their impacts. Finally, as a control measure, classical biological control has been much studied and applied to manage pests and less so to control pathogens (but see Rigling and Prospero 2018). This approach certainly deserves more research in forest pathology, especially against invasive pathogens.

Conclusions

We have argued that to improve forest protection, insects and pathogens should be considered collectively. In addition, although traditionally considered separate disciplines, many tools and conceptual frameworks can and should be shared between forest entomology and pathology. To further facilitate such collaboration and increase its benefits, we make the following recommendations:

1. Research policy
    - An interdisciplinary approach including entomology and plant pathology, but also economics and social sciences, should be encouraged in all research projects dealing with the adaptation of forests to global change and, in particular, with the risks to forest health.
    - Specific research topics involving interactions between forest insects and pathogens should be prioritised, such as insect-vectored diseases (e.g. ambrosia beetles) and physiological host tree responses to multiple biotic stresses (e.g. priming effects, cross-talks between defence pathways).

2. Research implementation and development
    - Innovative tools should be designed together by plant pathologists and entomologists, such as pipelines for high-throughput molecular species identification, artificial intelligence in smart sensors for detection of non-native organisms (e.g. detecting VOCs) and generic models for risk analysis and spread prediction.
    - Science-based guidelines should be developed to provide new sustainable forest management alternatives aimed at reducing the vulnerability of stands to both pests and diseases.
    - Forest entomologists and forest pathologists should collaborate to improve biosecurity strategies, such as those targeting the movement of damaging organisms associated with live plants and wood products.

3. Capacity building
    - Forest entomologists and forest pathologists should work together to build multidisciplinary curricula to sensitise students to the need to consider forest risks in a holistic manner and to educate future managers in integrated forest protection.
    - Public plant health services could work with plant pathologists and entomologists to create early warning systems using citizen science to involve the public in tree health issues, including opportunities for learning and participation in scientific research, monitoring and surveillance.
    - Entomologists and plant pathologists stand ready to assist decision- and policy-makers and forest managers in building global databases related to biological invasions, which will comprise information about threats, latest data on ongoing invasions, protocols and methodologies for eradication of emerging pests and pathogens, vectors of invasion and best practices for prevention.

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Authors' contributions

HJ, MLDL, AB, EGB, AS and JS designed the opinion paper and wrote the first draft, with subsequent contributions by all other authors.

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